Received: 10 October 2018 | Revised: 28 June 2019 | Accepted: 5 July 2019

DOI: 10.1111/jbi.13671

RESEARCH PAPER

Journal of Biogeography | WILEY

Similar compositional turnover but distinct insular environmental and geographical drivers of native and exotic ants in two oceans

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Funding information
Stellenbosch SubCommittee B; South African Research Chair Initiative; Universitat de Girona, Grant/Award Number: MPCUdG2016/084; Centre of Excellence for Invasion Biology; National Research Foundation, Grant/Award Number: 109244 and 89967

Handling editor: Daniel Chapman

Abstract

Aim: This study aims to quantify the patterns in compositional turnover of native and exotic ants on small islands in two oceans, and to explore whether such patterns are driven by similar environmental, geographical and potentially biotic variables.

Location: Pacific and Atlantic islands.

Time period: Present.

Major taxa studied: Ants.

Methods: We applied Multi-Site Generalised Dissimilarity Modelling (MS-GDM), which relates zeta diversity, the number of species shared by a given number of islands, to differences in environmental, geographical and biotic drivers. The use of zeta diversity enabled us to differentiate the contribution of rare species (shared by few islands) from those of widespread ones (shared by multiple islands) to compositional turnover. For completion, we also related species richness of insular ants per island with the same set of explanatory variables using Generalised Additive Models (GAM).

Results: Pacific and Atlantic islands have similar patterns of ant species turnover and richness, albeit partly driven by different drivers. Native and exotic species turnover are mostly explained by the same set of variables in the Pacific (annual precipitation and distance to the nearest island), but not in the Atlantic (annual precipitation is a good predictor of native species turnover, but none of the variables considered in our study explained exotic species turnover). No signal of biotic interactions was detected at the insular community level.

Main conclusions: Successful invasion strategies may depend on a combination of factors specific to the region in question. In the Pacific, milder environments and the absence of natives on certain islands enable exotic ants to select the same types of environment as native ants. In the harsher Atlantic Ocean, however, native ant species are likely to be well adapted to local environmental conditions, making it harder for exotics to become established. Exotic ant species, therefore, potentially rely on other attributes to establish, such as a combination of tolerance to a wide range of environmental conditions and human-mediated colonization.

KEYWORDS
ants, biodiversity, biotic interactions, environmental filtering, island biogeography, isolation by distance, Multi-Site Generalised Dissimilarity Modelling, species richness, species turnover, zeta diversity

1 | INTRODUCTION

For more than 50 years, islands have offered an invaluable context to study the organization of biodiversity. Given the acceleration in the human-mediated introduction and spread of exotic species into novel environments (Hui & Richardson, 2017), many have looked upon island ecosystems for additional insights into invasion ecology (Moser et al., 2018; Santos, Field, & Ricklefs, 2016). To date, studies on insular biological invasions have mostly focused on understanding the relationship between island characteristics and insular community structure, such as species richness (Blackburn, Delean, Pyšek, & Cassey, 2016; Kalmar & Currie, 2006; Moser et al., 2018), endemism (Rosindell & Phillimore, 2011) and species–area relationships (Matthews, Guilhaumon, Triantis, Borregaard, & Whittaker, 2016). Such studies ignore the compositional variation in species assemblages across different islands.

Islands are often not entirely isolated from each other. Prospective resident species with high dispersal abilities can establish themselves in an island following direct migration from the nearest continent, or through the exchange of propagules with established populations of other nearby islands. Insular assemblages composed of species with various dispersal abilities are, therefore, organized as sets of metacommunities (Leibold & Chase, 2017), in which population of species with low dispersal ability will operate largely independently on each island, whereas, at the other extreme, populations with high dispersal abilities will approach panmixia. As such, richness-based metrics cannot be considered in isolation, with growing awareness highlighting the possibility of drastic compositional changes without altering species richness (Dornelas et al., 2014). Investigating differences in species composition (i.e. compositional turnover) between islands is necessary to understand how community assembly processes affect insular biodiversity (e.g. Carvalho & Cardoso, 2014). That is, knowing *which* species are present (species composition and turnover) is more informative than knowing *how many* species are present (species richness; Hillebrand et al., 2018).

Multiple factors can affect compositional turnover between islands. The spatial distribution of islands and the dispersal capacity of species influence the exchange of propagules between islands. Even low levels of dispersal are known to potentially reduce species turnover (Declerck, Winter, Shurin, Suttle, & Matthews, 2013). The environmental conditions also influence the survival and establishment of introduced species (Hui & Richardson, 2017). *Isolation by distance* (species turnover emerges from dispersal limitation and islands distribution – IBD hereafter; Wright, 1943) and *environmental filtering* (species turnover reflects environmental gradients – EF hereafter), together with *biotic interactions* between native and exotic communities (BI hereafter), can, therefore, jointly affect species composition at different spatial scales (Meynard et al., 2013). Despite some studies investigating the role of EF and IBD to determine insular metacommunity structure at global scale (e.g. Roura-Pascual, Sanders, & Hui, 2016), studies revealing how changes in multiple factors influence species composition at the ocean or archipelago scale are rare. Previous work has, for example, shown that species mobility and, therefore, IBD was the most important driver of spider species turnover between Macaronesian islands (Carvalho & Cardoso, 2014).

An important conclusion from recent island biogeographic studies is that widespread (i.e. spatially common) and rare species are often driven by different assembly processes (e.g. Ulrich & Zalewski, 2006). This urges researchers to differentiate compositional turnovers of widespread species from those of rare species. However, compositional turnover is usually computed only between pairs of sites using different indices of beta diversity (Baselga, 2010), as exemplified by Generalised Dissimilarity Modelling (GDM; Ferrier, Manion, Elith, & Richardson, 2007). Such pairwise beta diversity captures predominately the contribution of species with low occupancy (referred to as rare species hereafter, not to be confused with species with low abundance) to turnover, and inadequately quantifies turnover from widespread species. In contrast, zeta diversity (Hui & McGeoch, 2014), the number of species shared by any given number of sites, allows us to disentangle the contribution of rare and widespread species to compositional turnover. The combination of zeta diversity and GDM, namely Multi-Site Generalised Dissimilarity Modelling (MS-GDM; Latombe, Hui, & McGeoch, 2017), therefore, provides an information-rich approach for teasing apart how the relationship between turnover and its covariates changes with the spatial commonness and rarity of species.

Using MS-GDM and Generalised Additive Models (GAM; Hastie & Tibshirani, 1990), we explore how the turnover and richness of native and exotic ant communities differ, and whether these patterns are driven by consistent geographical, environmental and biotic drivers across oceans. The comparison of these drivers can provide insights on the strategies used by exotic species to invade novel environments and on how natives and exotics may interact with each other. We distinguish at least three community assembly scenarios. First, if compositional turnovers of native and exotic ants are driven by the same set of environmental and geographical variables, the turnovers would also be correlated, suggesting that species from these two categories have similar niches and, therefore, may interact through indirect interactions such as exploitative competition for common resources. Second, if the turnovers of native and exotic ants are driven by different sets of

environmental and geographical variables, the turnovers are correlated (i.e. zeta diversity of natives explains that of exotics), that would be indicative of distinct niches between these two categories of species, and that the correlation may reflect the action of factors such as direct BI from interference competition. Finally, if the turnovers of these two categories of species are driven by different sets of environmental and geographical variables, and the turnovers are not correlated, that would suggest that exotic species rely on different strategies from natives to invade, and that the two categories of species seldom interact. Since the Pacific and Atlantic islands have different spatial distributions and experience different environments, studying them separately sheds new light on the context-dependent processes driving native community assembly and biological invasions.

When the turnover of native and exotic species is explored separately, we expect geographical variables (and, therefore, IBD) to better explain the turnover of native than exotic species, as the dispersal of exotic species has often been facilitated by humans, which would be consistent with the aforementioned third scenario. This aided dispersal has given exotics a colonization advantage that can boost the chance of establishment in otherwise remote islands, and, therefore, creates more stochasticity (uncertainty) in their distributions (Hui et al., 2013). We also expect, nonetheless, the relative importance of both IBD and EF to depend on the spatial distribution of the islands (IBD should be more important if islands are far from each other) and the environmental gradients (EF should be more important if islands have very different environmental conditions), and thus differ between the two oceans. Although BI has been shown to play some role for the establishment of specific exotic ant species, especially highly successful ones (Fisher, 2010; Suarez, McGlynn, & Tsutsui, 2010), it is unclear how that may impact the whole community and if there should be differences between the two oceans.

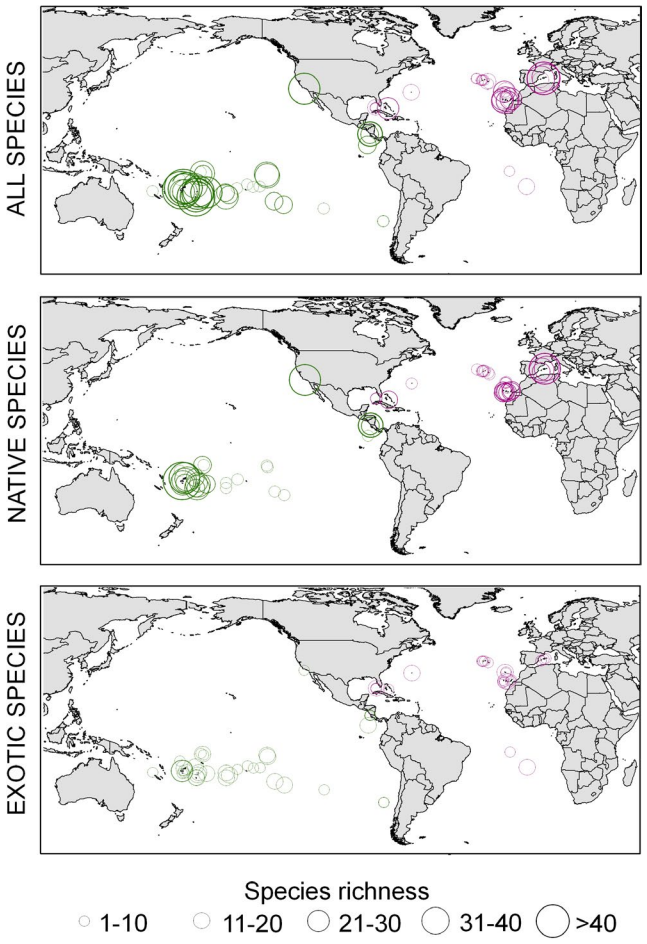

FIGURE 1 Map of the 42 Pacific and 36 Atlantic islands considered in the study. The Mediterranean's Balearic Islands were included in the Atlantic islands group due to their spatial proximity and the connection between the Mediterranean Sea and the Atlantic Ocean through the Strait of Gibraltar. The size of the symbols represents the ant richness of the islands for the subset of species considered (All, Natives, Exotics)

2 | MATERIALS AND METHODS

2.1 | Data

Presence–absence data of native and exotic ant species were compiled for 102 small islands (<1,000 km^2) worldwide by Roura-Pascual et al. (2016), from which we selected two subsets of islands based on the limits of their oceanic waters (i.e. oceanic borders; Figure 1): islands in the Pacific Ocean (hereafter 'Pacific islands') and islands in the Atlantic Ocean and the Mediterranean Sea (hereafter 'Atlantic islands') (see Appendix S1.1 for details on data acquirement and treatment).

Variables related to climate (mean annual temperature and annual precipitation) and habitat (using island area as a proxy for habitat diversity), which have been shown to impact ant community composition worldwide (Gibb et al., 2015), were used as environmental variables (i.e. as EF variables). Distance to the nearest continent, distance to the nearest island, the number of islands in a 300-km radius and the oceanic currents were used as geographical variables to characterize the spatial isolation of each island (i.e. as IBD variables; Appendix S1.1).

2.2 | Patterns of compositional turnover

Zeta diversity (Hui & McGeoch, 2014) combines the average number of species per island (i.e. species richness, ζ_1), and the average number of species shared by any number of islands (ζ_2 for two islands, ζ_3 for three islands, etc.). The number of islands used for calculating zeta diversity will hereafter be called the 'order of zeta'. As the order of zeta increases, zeta values necessarily decrease, and comparing zeta values for multiple orders (i.e. for different numbers of islands) enables us to differentiate the contribution of rare species (shared by only few island and, therefore, captured by low orders of zeta, e.g. ζ_2), and widespread ones (captured by high orders of zeta; see Appendix S1.2 for details on zeta diversity).

Two kinds of information can be obtained from the zeta values: the *magnitude* of the zeta values is related to species richness (since

a rich area will tend to have more species shared by multiple sites), and the *shape of the zeta diversity decline* provides information on the structure of turnover. A steep decline of zeta values at low orders indicates that turnover is mostly structured by differences in rare species composition between islands. A shallow decline denotes a structure mostly driven by common species. Differences in shapes of the tail of the zeta decline, where values are approaching zero, are hard to observe visually. The tails of the zeta decline can be more precisely compared using the *zeta ratio* ζ_n/ζ_{n-1}, indicating the rate at which species are retained as additional islands are considered (hereafter, the retention rate; McGeoch et al., 2019). The zeta order at which the zeta ratio values start declining indicates the number of islands after which common species are not retained as additional islands are considered.

The zeta diversity decline fits a composite parametric form combining an exponential and power law component:

$$\zeta_n = a \times \exp(-b \times n) \times n^{-c}, \quad (1)$$

where a, b and c are positive numbers, and can vary for different ranges of zeta orders n (i.e. a piecewise function; see Appendix S1.2 for conceptual and computational details). The relative parameter values of the exponential and power law components indicate whether a community assembly is predominantly stochastic or indicative of differentiation in species preference for specific sites respectively (Hui & McGeoch, 2014; Kunin et al., 2018). Differences in parameter values permit quantifying differences between the zeta declines.

2.3 | Drivers of multi-site compositional turnover

Multi-Site Generalised Dissimilarity Modelling (Latombe et al., 2017) was used to evaluate how the number of species shared by specific $n \geq 2$ islands (hereafter noted $\tilde{\zeta}_n$, where $\zeta_n = \text{mean}(\tilde{\zeta}_n)$) changes with differences in environmental and geographical variables. MS-GDM relates $\tilde{\zeta}_n$ to the average differences in environmental and geographical variables between these n-specific islands, and assesses this relationship by using multiple combinations of islands. It differs from the calculation of zeta diversity described above in that zeta diversity averages the number of shared species across all possible combinations of n islands, while MS-GDM examines the relationship between shared species and variable differences for specific combinations of n islands. $\tilde{\zeta}_n$ was divided by the minimum richness in any of these n islands, that is, similar to Simpson dissimilarity, to assess the drivers of richness-independent turnover (see Appendix S1.3 for details on the computation of MS-GDM, and Appendix S4 for analyses and results using the Sørensen version of zeta diversity).

In addition to the environmental and the geographical variables used to assess the effect of EF and IBD, the $\tilde{\zeta}_n$ of native species for the n-specific islands were also incorporated into MS-GDM as an explanatory variable for the $\tilde{\zeta}_n$ of exotic species in a second set of analyses to examine the influence of BI (see Appendices S1.3 and S5 for computational details and results). Doing so enabled us to test the potential presence of direct BI between native and exotic species (such as interference competition) and their impacts on insular assemblage compositions (Latombe, Richardson, Pyšek, Kučera, & Hui, 2018). Analyses for exotic species were, therefore, performed with and without native zeta diversity as an explanatory variable.

Note that MS-GDM must be computed separately for each order $n > 2$ of zeta, which enables us to differentiate the drivers of species turnover for rare versus widespread species (see Appendix S1.3 for justification and details). In particular, MS-GDM was applied to each ocean separately for zeta order 2–5 (i.e. using combinations of two to five islands) for native and exotic species separately. When more than five islands are considered, the average number of shared species is below 1, indicating a nearly complete species turnover, making the inference of the relationship with environmental, geographical and biotic variables problematic. For each MS-GDM (i.e. for each order of zeta, and for each species category in each ocean), we computed the variance explained as the Pearson R^2 between the observed zeta values $\tilde{\zeta}_n$ and zeta values predicted by the model for 5,000 combinations of n islands, as the absolute performance of each model. This was performed for 30 replicates, using a different set of 5,000 combinations for each replicate.

For each order of zeta, MS-GDM generates a monotonic, nonlinear I-spline for each explanatory variable (Appendix S1.3). Two features of I-splines are informative: the relative amplitude of I-splines (i.e. their maximum values relative to each other), and changes in the slope of I-splines. The relative amplitude of a spline indicates the overall effect of the variable on zeta diversity relative to the other covariates. A high amplitude for environmental variables would indicate that species distributions across islands are constrained by environmental heterogeneity (i.e. compositional turnover emerges from EF). A high amplitude for geographical variables would indicate that species distributions across islands are constrained by their dispersal capacity (i.e. compositional turnover emerges from IBD; Wright, 1943). A high amplitude for native zeta values would indicate that compositional turnover are constrained by BI between native and exotic species (BI).

In contrast, changes in the slope of an I-spline indicate the values where differences in the corresponding explanatory variable are important to compositional turnover. A steeper slope corresponds to a greater effect. For example, a steep slope at low precipitation values would indicate that difference in precipitation is important in dry environments. A shallow slope at high precipitation values would indicate that the same difference in precipitation in wet environments is not important.

2.4 | Drivers of species richness

To broaden the description on biodiversity drivers, the relationship between insular richness (i.e., $\tilde{\zeta}_1$) and the environmental, geographical and biotic variables described above was also assessed for each

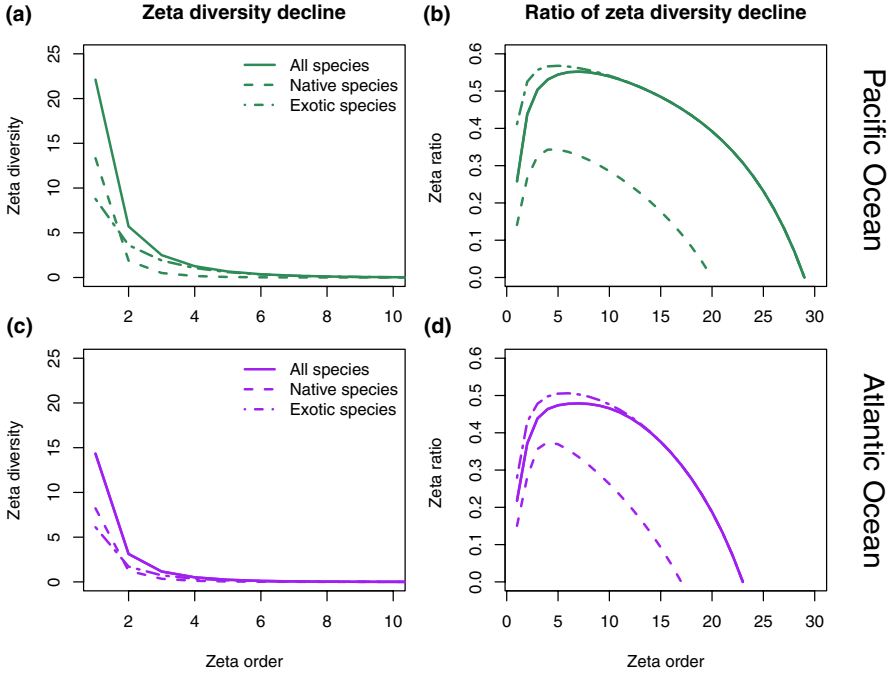

FIGURE 2 Decline of zeta diversity (a,c) and retention rate (b,d) for all, native and exotic species for the Pacific (a,b) and Atlantic (c,d) island groups. The ratio of zeta diversity (the retention rate) is computed as ζ_n/ζ_{n-1}. Only orders 1 to 10 are shown in the zeta decline for clarity

TABLE 1 Summary of the GAM and Multi-Site Generalised Dissimilarity Modelling (MS-GDM) outputs, indicating the most important variables for explaining insular species richness ($\tilde{\zeta}_1$) and compositional turnover ($\tilde{\zeta}_{n\geq 2}$). See Figures 4 and 5 and Figures S2.4–S2.9 in Appendix S2 for the detailed corresponding graphics

	Pacific		Atlantic	
	Native	Exotic	Native	Exotic
Annual precipitation	$\tilde{\zeta}_{2-5}$	$\tilde{\zeta}_{2-3}$	$\tilde{\zeta}_{1-5}$	$\tilde{\zeta}_{1-5}$
Mean annual temperature		$\tilde{\zeta}_{1,4-5}$		$\tilde{\zeta}_{4-5}$
Island area	$\tilde{\zeta}_1$	$\tilde{\zeta}_1$	$\tilde{\zeta}_1$	$\tilde{\zeta}_1$
Distance	$\tilde{\zeta}_{2-5}$		$\tilde{\zeta}_{2-5}$	
Nearest continent	$\tilde{\zeta}_1$		$\tilde{\zeta}_1$	$\tilde{\zeta}_1$
Nearest island	$\tilde{\zeta}_{1-5}$	$\tilde{\zeta}_{2-3}$		$\tilde{\zeta}_1$
Number of islands in vicinity		$\tilde{\zeta}_1$	$\tilde{\zeta}_1$	$\tilde{\zeta}_{4-5}$
Oceanic current		$\tilde{\zeta}_{2-3}$		

Note: Distance and oceanic current were not used as explanatory variables for explaining richness in the GAM.

ocean using Generalised Additive Models (GAM; Hastie & Tibshirani, 1990) (Appendix S1.4).

3 | RESULTS

3.1 | Patterns of compositional turnover

The Pacific and Atlantic Oceans present similar zeta diversity declines of native and exotic ant species (Figure 2). It is indicative of similarities on three characteristics of native and exotic species diversity between the two oceans (see Appendix S3 for details): (a) The average species richness per islands (ζ_1) was higher for natives than for exotics in both oceans (Figure 2a,c); (b) The number of exotic species shared by multiple islands (ζ_n, $n \geq 2$) was higher than the number of natives in both oceans (Figure 2a,c); (c) The retention rate of exotic species was higher than for native species, indicating a proportionally slower decline of zeta values and thus a higher proportion of widespread species for exotics (Figure 2b,d). The estimated parameters of Equation 1 quantitatively confirm the similarities in turnover between the two oceans, exhibiting a switch from a composite (non-random structure) to an exponential (random structure) form as the order of zeta increases (Table S2.1, Appendix S3.1).

3.2 | Drivers of multisite compositional turnover

The environmental and geographical variables explained the turnover of native and exotic species equally well in the Pacific ($.381 < R^2 < .592$, decreasing from zeta order 2–5 for natives; $.325 < R^2 < .523$ decreasing from zeta order 2–5 for exotics; Table 1; Figure 3). In the Atlantic, the explanatory variables explained the turnover of native species at a similar level ($.346 < R^2 < .635$ decreasing from zeta order 2–5), but the variance explained was lower for exotic species ($.230 < R^2 < .259$ across zeta orders 2–5; Table 1; Figure 3). This low variance explained indicates that, contrary to the other three categories (natives and exotics in the Pacific and natives in the Atlantic), exotic species turnover is not explained by the environmental or the geographical variables in the Atlantic Ocean. Including native zeta diversity as an explanatory variable for exotic zeta diversity did not increase notably the variance explained by the models in either ocean (Appendix S5).

For native species, the distance between islands is by far the main driver of species turnover in both oceans and for all orders of zeta, as shown by the high amplitude of its I-spline compared to the

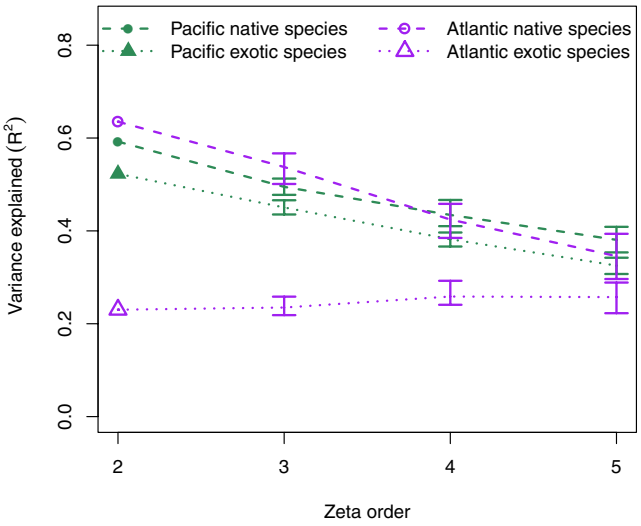

FIGURE 3 Percentage of variance explained by the environmental and geographical variables using Multi-Site Generalised Dissimilarity Modelling for Simpson zeta diversity for the two oceans and species groups, computed as the square of Pearson coefficient between observations and predictions. The error bars represent the standard deviation of the R^2 over 30 replicates. Since there are less than 5,000 combinations of two islands for both oceans, no error bar was generated for $\tilde{\zeta}_2$

other variables (Figure S2.4). In the Pacific, the difference in precipitation in dry environments (i.e. in environments with low precipitation, as shown by the steep slope of the I-spline for low precipitation values) is the second main driver of native species turnover for all orders, followed by the difference in distance to the nearest island, especially when the distance is small, as shown by the sharp initial slope (Figure 4). In the Atlantic, differences in precipitation and the difference in distance to the nearest island are also the main drivers of zeta values for orders 2 and 3 (i.e. compositional turnover of relatively rare species), secondary only to the distance between islands (Figure 4). The high amplitude of the spline for distance to the nearest island is caused by a few isolated islands in the data evident from the large gap between percentile symbols towards the large-distance end. For orders 4 and 5 (i.e. for compositional turnover excluding the rarest species) difference in mean annual temperature becomes the main driver at high temperature, as shown by the sharp slope at high values only, and the amplitude (the maximum value) of the I-spline is more than twofold compared to precipitation. In all cases, the splines with a high amplitude also have low variability across replicates, confirming the importance of the corresponding variables for explaining species turnover (Figure S2.6).

For exotic species on Pacific islands, just as for natives (when excluding distance between islands), a difference in precipitation in dry environments is the main driver of species turnover across all orders of zeta (Figure 5). In contrast, however, geographical variables have a smaller effect on species turnover, relatively. For the Atlantic islands, difference in precipitation is the main driver for low orders of zeta (Figure 5). However, contrary to native species, difference in precipitation matters for wet rather than for dry environments, as shown by the steep slope of the spline for large precipitation values. As the order of zeta increases, so does the importance of mean annual temperature (as for native species) and number of islands in a 300-km radius (as shown by the increase in amplitude of the corresponding spline). Note, however, that the explained variance for the Atlantic exotics is low (~20%; Figure 3), especially for low orders of zeta, indicating that other factors are important to explain species turnover, and these I-splines should be interpreted with caution.

3.3 | Drivers of species richness

Insular species richness was well explained by the variables included in the analyses (Appendix S3.2, Figures S2.10 and S2.11). Island area was the most common variable to be positively related to richness for both natives and exotics in both oceans (Figures S2.10 and S2.11). There were nonetheless marked differences in the other drivers in the two oceans. Native richness was only significantly positively related to exotic richness in the Pacific islands. In the Pacific, distance to the nearest continent and distance to the nearest island were negatively related to native richness, but not to exotic richness. Temperature was only positively related to exotic richness.

In the Atlantic, distance to the nearest continent was negatively correlated with both native and exotic richness. Counter-intuitively, distance to the nearest island was positively related to insular exotic richness, whereas we would expect proximity between islands to increase the exchange of propagules and, therefore, species richness. Precipitation in dry areas was positively related to native richness, whereas it was negatively related to the exotic in wet areas.

4 | DISCUSSION

Our results show that, although the Pacific and Atlantic oceans have very similar patterns of zeta decline for both native and exotic compositional turnover (Figure 2), there are large differences between the two oceans when comparing the drivers of turnover for native and exotic ant species (Table 1; Figures 3–5; Figures S2.6–S2.9), pointing at different community assembly processes as related to EF, IBD and potentially BI. This study, therefore, provides refined insights into the drivers of biological invasions of islands and highlights the importance of the specificities of each ocean for invasion and compositional turnover, compared to global-scale works on general relationships between native and exotic diversity, without accounting for regional context (e.g. Blackburn et al., 2016; Roura-Pascual et al., 2016).

4.1 | Similar patterns but contrasting processes

Based on the observed patterns of zeta diversity declines alone, insular ant communities in the Pacific and Atlantic appeared to be strikingly similar, both qualitatively and quantitatively. In both oceans, the average native richness per island was higher than exotic richness, due to a few islands harbouring high native biodiversity (Figure

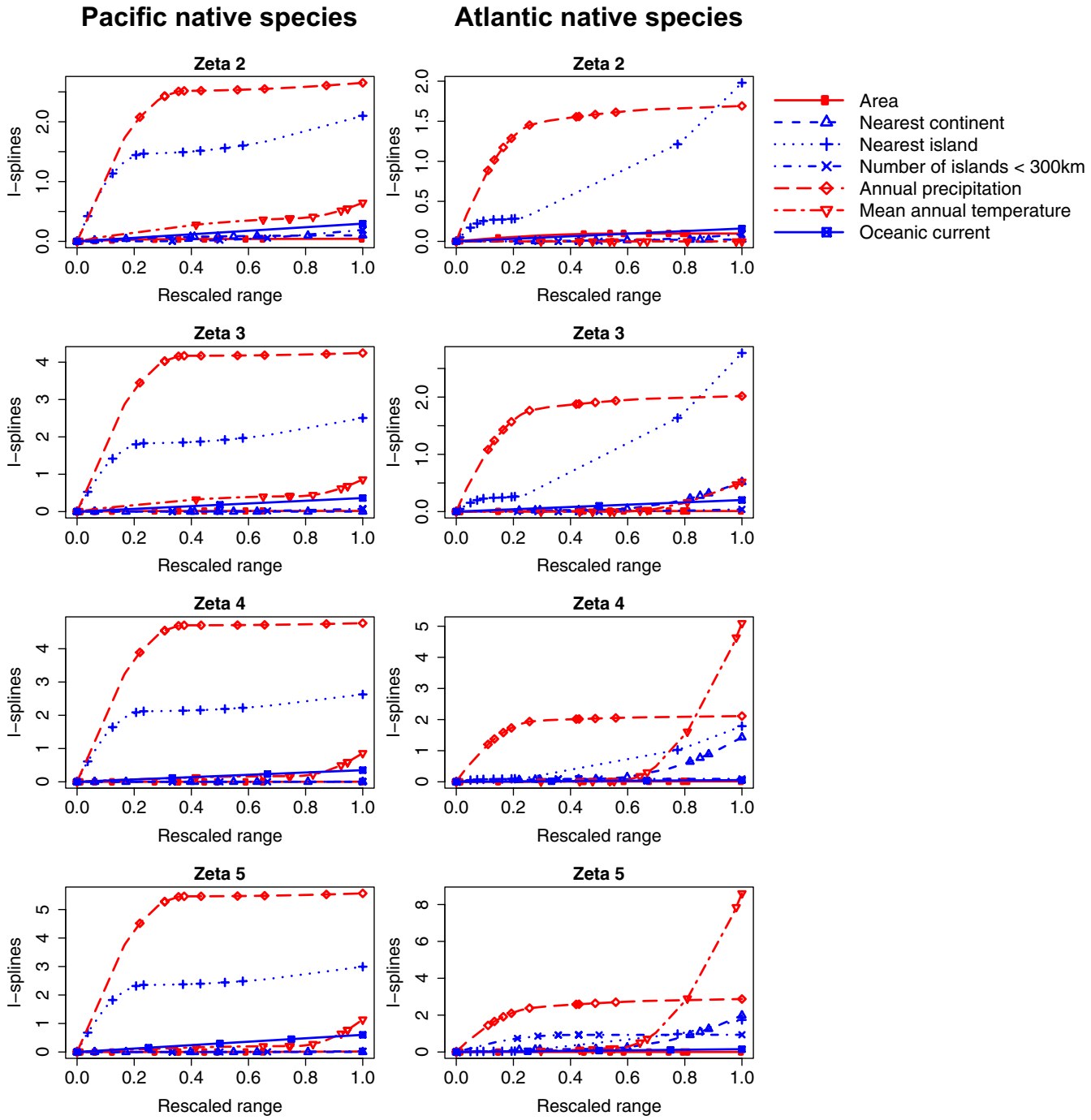

FIGURE 4 I-splines computed with Multi-Site Generalised Dissimilarity Modelling for native species of the Pacific and Atlantic island groups, from $\tilde{\zeta}_2$ to $\tilde{\zeta}_5$ for Simpson zeta diversity (averaged over 30 replicates – see Appendix S2.3; Figures S2.6 and S2.8). The horizontal axes represent the original variables, rescaled between 0 and 1 for comparison (see Tables S2.2 and S2.3 for the scaling factors – environmental variables are in red and geographical ones are in blue). The vertical axes represent the transformed variables, combining the three I-splines I_k for each variable after fitting Equation S1.2 (see Appendix S1.2 for mathematical details). The relative amplitude of each spline in a given panel, therefore, represents the relative importance of the corresponding variable to explain zeta diversity for a specific order. For each variable, the symbols are located at the percentiles, providing information on the distribution of values. Distance between islands was computed in the analyses, but is not presented here due to its over dominance (See Figure S2.4 including the distance between islands)

S2.2), but islands generally shared more exotic than native species (Figure 2a,c) because, on average, exotics are more widespread than natives (Figure S2.3). The difference was slightly more marked for the Pacific, as demonstrated also by the differences in the retention rate between natives and exotics (Figure 2b,d), but this is partly due to some Pacific islands being more remote and not having any native ants. The intersection of zeta decline curves between orders 1 and 2 indicates that certain native ant species co-occur more strongly

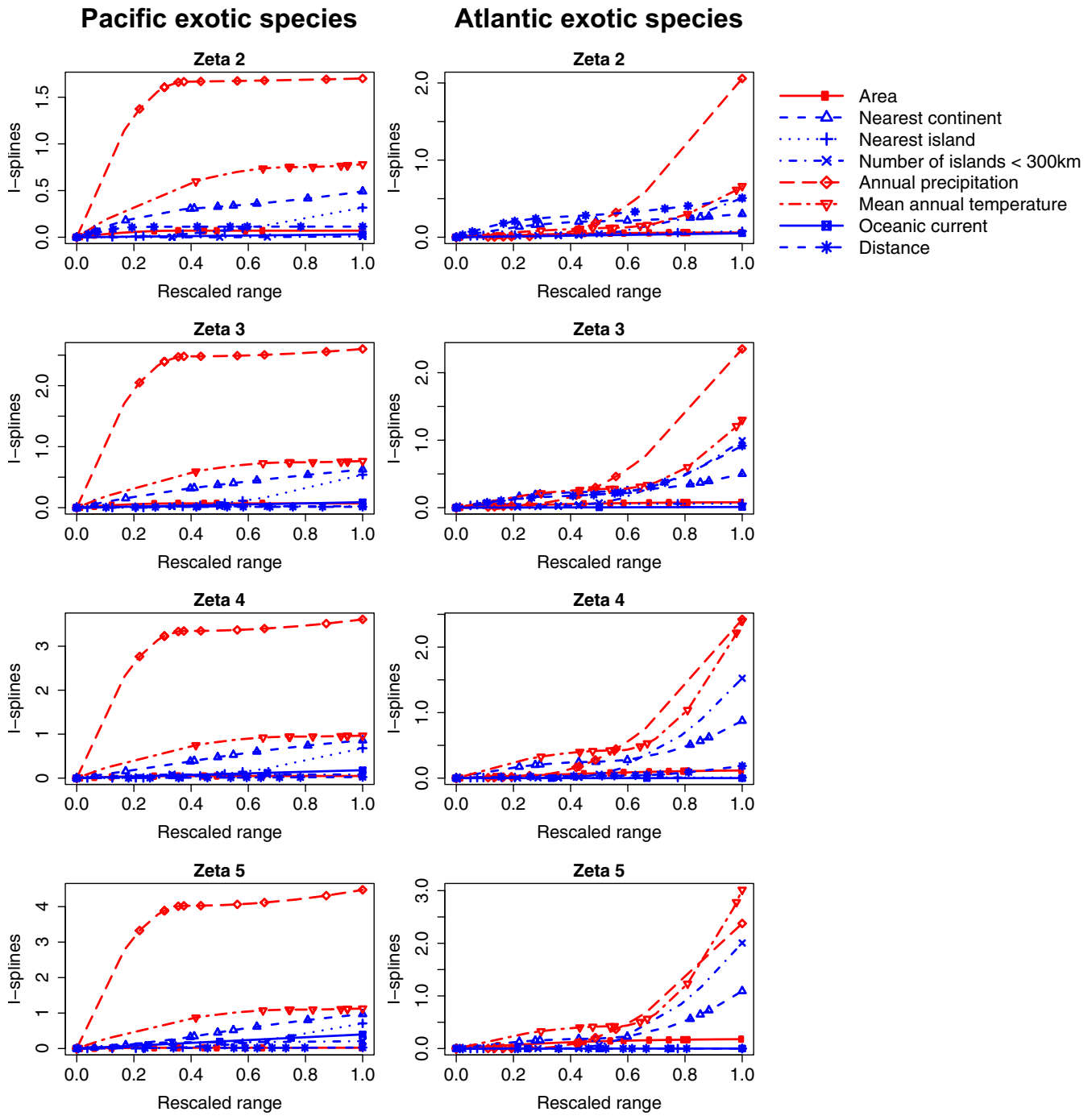

FIGURE 5 I-splines computed with Multi-Site Generalised Dissimilarity Modelling for exotic species of the Pacific and Atlantic island groups, from $\tilde{\zeta}_2$ to $\tilde{\zeta}_5$ for Simpson zeta diversity (averaged over 30 replicates – see Appendix S2.3; Figures S2.7 and S2.9). The horizontal axes represent the original variables, rescaled between 0 and 1 for comparison (see Tables S2.2 and S2.3 for the scaling factors – environmental variables are in red and geographical ones are in blue). The vertical axes represent the transformed variables, combining the three I-splines I_k for each variable after fitting Equation S1.2 (see Appendix S1.2 for mathematical details). The relative amplitude of each spline in a given panel, therefore, represents the relative importance of the corresponding variable to explain zeta diversity for a specific order. For each variable, the symbols are located at the percentiles, providing information on the distribution of values

than exotic species. This confirms the higher modularity in native over exotic ant communities observed by Roura-Pascual et al. (2016), as exotic species are known for being better dispersers, especially because of human activity (Fisher, 2010; Hulme et al., 2008; Suarez et al., 2010).

Despite the similarities in the zeta declines of native and exotic species for both oceans, the GAM and MS-GDM analyses show that the patterns of richness and turnover are partly driven by different variables. Consequently, considering only patterns of turnover, without further comparing community assembly drivers, could be misleading

to understand community assembly. Island area was the main driver of species richness for natives and exotics in both oceans (Figures S2.10 and S2.11), as predicted by the Equilibrium Theory of Island Biogeography (MacArthur & Wilson, 1967), while precipitation was important for species turnover (Table 1; Figures 4, and 5). However, there were also marked differences, as shown by the differences in variance explained (Table 1; Figure 3) and by the different shapes of the I-splines relating zeta diversity to environmental variables (Figures 4 and 5). For example, temperature mattered in the Atlantic for zeta orders ≥4, whereas precipitation was more important in the Pacific for both natives and exotics across zeta orders. In contrast, richness depends on temperature in the Pacific, but on precipitation in the Atlantic (Figure S2.10). Different variables, therefore, explain richness and compositional turnover, showing the necessity of considering both patterns and assembly processes of biodiversity.

Biotic interactions are known to influence the success of exotic ants (Fisher, 2010; Suarez et al., 2010), but the mechanisms by which it happens are often unclear and vary depending on the invading species, the characteristics of the native ant community and other environmental variables (Cerdá, Arnan, & Retana, 2013; Holway, Lach, Suarez, Tsutsui, & Case, 2002). The fact that native species richness was positively related to exotic richness in the Pacific, but not in the Atlantic (Figures S2.10 and S2.11) may support this fact. The positive correlation in the Pacific was, however, relatively weak for most islands, as shown by the initial shallow slope of the GAM (Figure S2.10), and strongly driven by the inclusion of Viti Levu (the largest Pacific island, with the highest native and exotic richness). Using the native richness as an explanatory variable also reduced the importance of island area to explain exotic richness, due to the correlation between native richness and island area. Moreover, using native zeta diversity as an explanatory variable for exotic zeta diversity in MS-GDM did not increase the variance explained in any of the two oceans (Appendix S5). Such BI may, therefore, be species- and site-specific, and hardly detectable at the whole metacommunity scale. We, therefore, only discuss the role of EF and IBD below.

4.2 | EF: Do exotic and native species play by the same rules?

The fact that the turnover of both native and exotic ants is mostly explained by precipitation, and that the variance explained for these variables is similarly high in the Pacific (Table 1; Figures 3–5) suggests that the native and exotic species that compose these communities may have similar abiotic niches. This may be due, for example, to environmental filters forcing exotics to adopt similar traits and distributions as natives (Rouget, Hui, Renteria, Richardson, & Wilson, 2015). The importance of precipitation (Table 1; Figures 4 and 5) is consistent with the wide range of precipitation values in the Pacific islands (Figure S2.1). This diversity of precipitation regimes provides ample niche opportunities for exotic species, consistent with the available niche hypothesis (Shea & Chesson, 2002). In addition, 11 out of 42 Pacific islands contain no native species (Figure S2.2), leaving, therefore, only abiotic constraints for exotic species to establish themselves. The fact that exotic species could colonize islands with no native species probably also explains why native and exotic richness were mostly explained by different variables, with the exception of island area, since these native-free islands were likely to have slightly different environmental and geographical conditions than the occupied islands due to distinct geographical locations.

In contrast, there is large difference in variance explained by the environmental and geographical variables for natives and exotics in the Atlantic. None of these variables could explain the turnover of exotic species, as shown by the low variance explained (Figure 3), contrary to that of native species, for which precipitation (as in the Pacific) but also temperature (for orders ≥4) played an important role (Table 1; Figures 3–5). Without ruling out the chance of missing important variables, this suggests that exotic species in the Atlantic may have wider abiotic niches or higher phenotypic plasticity and be tolerant to a wide range of environmental conditions, which has been observed for other invertebrates (Chown et al., 2007).

Differences in environmental conditions, especially temperature and precipitation regimes, could be behind the contrasting strategies used by exotic species in the two oceans. Climatic conditions are harsher in the Atlantic islands, with lower temperature and precipitation (Figure S2.1). Specific native ant species in the Atlantic are, therefore, likely to be well adapted to local environmental conditions, making it harder for exotics to become established. Moreover, the relationship between precipitation and richness showed opposite trends for exotics and natives, although precipitation is the only environmental variable showing a significant relationship for both categories of species in the Atlantic. Exotic ant species, therefore, potentially rely on other attributes to get a competitive edge, such as a colonization advantage.

4.3 | IBD: The competition–colonization trade-off

As expected, geographical variables related to IBD had a stronger impact on native than on exotic species richness and turnover in both oceans. Distance to the nearest continent (and to the nearest island) is negatively correlated with native richness in both oceans, more strongly than with exotic richness (Figure S2.10 and S2.11). IBD also explains native turnover between islands better than alien turnover. The distance between islands is especially important for native turnover (Figure S2.4), reflecting the sudden cut-off in the distance decay of similarity beyond which two islands do not share any native species (~7,000 km in the Pacific, ~4,000 km in the Atlantic; Figure S2.5). Difference in distance to the nearest island also strongly influences native species turnover (Figure 4). In contrast, exotic species are likely transported more by humans than through natural dispersal (Roura-Pascual et al., 2016; Suarez et al., 2010), thus breaking the IBD pattern and diminishing the influence of island geography. Some exotic species could have benefited from a colonization advantage that may compensate limited competitive ability, that is, the competition–colonization trade-off (Yu & Wilson, 2001; whereas highly successful exotic species, also termed 'invasive', are often considered to benefit from a combination of high competitive ability and other biotic and abiotic factors; Cerdá et al., 2013; Holway et al., 2002).

The importance of IBD for determining the distribution of exotic species is lower in the Atlantic than in the Pacific, as shown by the

difference in variance explained, and by the small effect of distance to the nearest continent and to the nearest island on exotic turnover in the Pacific (Figure 3). Most Atlantic islands considered here are part of archipelagos with thriving tourism industries, such as the Azores, the Canaries and Balearic Islands, and are located on major current and historical shipping routes (Halpern et al., 2008). They have, therefore, been subject to frequent exchanges of goods and people from Africa and Europe for millennia, whereas the Pacific islands are located in some of the most remote places on the planet (Morrison, 2014). Exotic species in the Atlantic probably have a greater colonization advantage through human-mediated dispersal, using immigration from both the continent and from other islands, irrespective of distance. As a result, this colonization advantage may be enough to enable their colonization success, even in islands with suboptimal abiotic environments and regardless of native species composition. That could explain the low variance explained by the environmental and geographical variables, even when using native zeta diversity as an explanatory variable for exotic zeta diversity (Appendix S5), and the lack of correlation between native and exotic richness (Figure S2.11). This human-mediated colonization advantage could also explain the positive relationship observed between exotic richness and distance to the nearest island. Large cargo ships may not have stopped at proximate islands but may have had systematic ports of call on remote islands for refilling supplies and fuel.

The spatial distribution of islands also likely plays an important role in the relative strength of EF and IBD variables for explaining species turnover. Given the importance of dispersal between local populations for the structure of metacommunities (Leibold & Chase, 2017; Mouquet & Loreau, 2002), the centrality of an island within an archipelago can be critical for determining its richness (Economo & Keitt, 2010). The Atlantic islands are spatially organized into three main clusters of high density (the Azores, the Canaries and the Balearic Islands) but greatly separated from each other (Figure 1; Figure S2.1h), potentially resulting in frequent dispersal and exchange of propagules within, rather than between, clusters (Fisher, 2010) – this in turn explains why each cluster has a distinct ant assemblage (Roura-Pascual et al., 2016). This spatial organization could explain the importance of distance between islands for explaining turnover for native species in the Atlantic compared to the Pacific for $\tilde{\zeta}_2$ and $\tilde{\zeta}_3$ (Figure 4). Note, the I-spline of distance between islands reaches a plateau at ~4500 km, corroborating the distance separating the clusters of islands (Figure S2.1h).

5 | CONCLUSION

We have shown that Pacific and Atlantic islands have similar patterns of ant species turnover between natives and exotics, and that both native and exotic turnover are driven mostly by the same variables in the Pacific, but not in the Atlantic. This difference may reflect divergences in the invasion strategies used by exotics, and may be determined by a combination of factors specific to the region of interest. In the Pacific region, with milder environments and about a quarter of islands having no native species, exotic ant turnover was driven by the same variables as native ant turnover, suggesting similar selection pressure. In contrast, the Atlantic region is drier and colder, which may have required native species to adapt to these harsher conditions, and forced exotic species to rely on different strategies to invade. In particular, the high density of shipping routes in this area may have facilitated the dispersal of exotic species and provided them with an 'artificial' colonization advantage strong enough to compensate for lower performance in the harsher environment of some islands, and, therefore, to reduce the importance of such abiotic variables for determining species composition.

Using several orders of zeta diversity shows that the similarity between drivers of natives and exotics in the Pacific and their difference in the Atlantic is consistent across several levels of rarity and commonness, although assemblages of widespread species (high orders of zeta) appear to be organized more randomly than rare ones. Considering various orders of zeta also enabled us to distinguish drivers of turnover for widespread species between the two oceans, as temperature becomes the primary driver for native turnover in the Atlantic for orders ≥4, with direct implications for designing, monitoring and management strategies to distinguish between rare and widespread species. It is nonetheless important to note that we do not recommend using one particular order of zeta diversity. It is the use and comparison of *multiple* orders of zeta that makes it informative. Considering the zeta diversity metric that encompasses but also extends the classical concepts of species richness and pairwise beta diversity, and acknowledging regional specificities, therefore, provides a more accurate perspective on the regional-scale drivers of biological invasions and community assembly.

ACKNOWLEDGEMENTS

We are grateful to Melodie A. McGeoch and David M. Richardson for conceptual discussions, and Xavier Espadaler for sharing the occurrence data. We thank Andrés Baselga and three anonymous reviewers for comments on a previous version of this article. GL acknowledges fellowships from the Centre of Excellence for Invasion Biology and the Stellenbosch SubCommittee B; CH acknowledges support from the South African Research Chair Initiative and the National Research Foundation of South Africa (Grants 89967 and 109244); NRP acknowledges support from the University of Girona (Grant MPCUdG2016/084).

DATA AVAILABILITY STATEMENT

All codes are included as supplementary material, and data available on request.

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How to cite this article: Latombe G, Roura-Pascual N, Hui C. Similar compositional turnover but distinct insular environmental and geographical drivers of native and exotic ants in two oceans. *J Biogeogr.* 2019;00:1–12. https://doi.org/10.1111/jbi.13671